Impacts of Demographic Variation in Spawning Success on Reference Points for Fishery Management

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Abstract.- Parametric relationships between recruitment and an index of parental stock size assume the latter is proportionally related to spawning potential (usually indexed by spawning biomass), irrespective of the demographic composition of adults. Recent empirical information, however, suggests that spawning by older, more experienced females is more successful than that by the young, small or inexperienced within a population. New models are proposed incorporating the proportion of the ith age class spawning for the jth time ($PSP_{i,j}$), from information contained in the maturity ogive, and experimental results relating the survival of eggs and larvae to the age, size or reproductive experience of adults. A series of spawning metrics (spawning stock biomass or *SSB*, egg production, hatched egg production, viable larval production) and associated recruitment-based fishing mortality reference points (F_{med}, $F_{crash} = F_{extinction} = F_{\tau}$) and the *F* that allows at least one lifetime spawning per recruit) are contrasted for the Georges Bank cod stock. We conclude: (1) the time series of cod spawning intensity is significantly altered when hatched eggs or viable larvae are used as the metric, reflecting the importance of first- and second-time spawners in some years, and the increasing trend in *F* over time, (2) percent maximum spawning potential (%MSP) curves in relation to fishing mortality are steeper (e.g. result in lower %MSP for a given *F*), when the metric is hatched eggs and viable larvae rather than *SSB* or egg production per recruit, (3) lifetime expected numbers of spawnings per recruit are significantly reduced when the effects of spawning experience on egg hatching success are included, and (4) the median *F* estimated from 5,000 bootstrap realizations of the Beverton-Holt *S-R* curve for viable larvae (*F*=0.88) is much lower than that from *SSB* (*F*=1.40), with narrower confidence bounds. Our results suggest that traditional approaches to *F*-based reference points using *SSB* systematically overestimate the resiliency of stocks to fishing. This adds impetus to the need for adopting precautionary approaches to fisheries management. Additional laboratory studies of the life history of spawners in relation to the fate of eggs and larvae are clearly warranted.

Introduction

A critical assumption of all models of stock and recruitment is that the effective spawning potential of the population is proportional to its index. Typically, spawning stock biomass (*SSB*) is used as the metric of spawning potential, but concerns have been raised recently that the proportionality assumption may not hold in cases where contributions to *SSB* are increasingly reliant on first- or second-time spawners or where the age composition of the *SSB* has undergone significant change (Chambers and Trippel 1997; Trippel et al. 1997a). In the case of western Atlantic groundfishes, severe depletions in fish abundance have occurred (Murawski et al. 1997), along with substantial reductions in the age and size at first sexual maturity (O'Brien et al. 1993; Trippel 1995; Hunt 1996; Trippel et al. 1997b), and a disproportionate loss of old, repeat-spawning fish (Myers and Cadigan 1995; Trippel 1995). Laboratory experiments on Atlantic cod, *Gadus morhua*, suggest that first-time spawners perform poorly compared to more experienced animals, breeding for a shorter period, producing fewer egg batches, exhibiting lower fecundity, and producing smaller eggs with lower fertilization and hatching rates (Solemdal et al. 1995; Trippel 1998). If these mechanisms are important in nature, then traditional approaches to evaluating harvest strategies based on recruitment vs. *SSB* data may overestimate the resiliency of stocks to

exploitation particularly since depleted or recovering fisheries may be dependent on inexperienced spawners to support population reproduction. In this study we incorporate some recent experimental findings on reproductive success in relation to spawner size/age and maternal experience, into alternative metrics of spawning potential. These alternative spawning metrics are used to re-calculate biological reference points related to recruitment failure and stock collapse (Smith et al. 1993; ICES 1997). The results of new models are contrasted with traditional approaches for the Georges Bank cod stock (Anonymous 1997).

Overview of Some Experimental Studies of Spawning Demographics

Two important factors in relating adult population structure to effective spawning potential of a stock are: (1) numbers of years that an iteroparous fish has previously participated in spawning (i.e., spawning experience), and (2) the relationship between spawner size/age and the quality of reproductive products (Trippel et al. 1997a). Trippel (1998) found that 13±6.7% of cod eggs hatched from first time spawners, compared to 62±4.4% from second-time spawners.

Models described below account for the differential effects of spawning experience by tracking each spawning platoon comprising each age group, identified by the age they begin breeding. In the case of Georges Bank cod, individuals may begin spawning anywhere from the first to the fifth year; there are thus up to five potential spawning platoons in each age group (Anonymous 1997).

A direct relationship between maternal age/size and egg diameter has been observed for cod (Kjesbu 1989; Solemdal et al. 1993; Solemdal et al. 1995; Chambers and Waiwood 1996; Kjesbu et al. 1996; Trippel et al. 1997a). Egg diameter has been positively correlated with several indices of cod egg and larval viability, including larval dry weight, yolk weight, percent of larvae comprised of yolk, hatching percentage (Trippel 1998), resulting larval length, percent of larvae feeding on day five, percent of larvae with a swim bladder on day 10, and specific growth rate (SGR as a percent) of 15-day-old larvae (Marteinsdottir and Steinarsson 1998). We chose to model the effects of maternal age/size on larval viability via a function relating spawner age to the percent of larvae with swim bladders at age 10 days (Marteinsdottir and Steinarsson 1998).

Our model strategy relates variation in hatching success to maternal experience, and variation in larval viability to age/size effects. Our analyses are primarily intended to illustrate the potential impacts of these assumptions on results of stock-recruitment analyses, and to motivate further experimental work.

Metrics of Spawning Potential and Biological Reference Points

Metrics of Spawning

Spawning stock biomass (*SSB*) is typically computed for iteroparous annual spawning species as:

$$SSB = \sum_{i=1}^{n} N_i \cdot \overline{WS_i} \cdot PM_i \qquad (1)$$

where N_i = numbers alive at spawning age i, determined by $N_i = N_{i-1} \cdot [\exp\text{-}\{F+M\}]$; $F_i = PR_i \cdot F$, where PR_i is partial recruitment to the fishery. The numbers of animals from the beginning of the calendar year to the spawning time is decremented by the fraction of $F+M$ that occurs before spawning. The oldest age is considered a plus group, for which the total lifetime contribution to the spawning population in numbers is given by: $1/[1\text{-}\exp(\text{-}\{F+M\})]$;

$\overline{WS_i}$ = mean weight (kg) at age for the stock;
PM_i = proportion of females, age *i*, that are sexually mature.

Population egg production (*EGGS*) is given by:

$$EGGS = \sum_{i=1}^{n} N_i \cdot E_i \cdot PM_i \qquad (2)$$

where E_i = mean fecundity (numbers of spawned eggs) at age *i*.

If hatching success is related to spawning experience, the calculation of the number of hatched eggs requires that numbers at age be subdivided into groups that vary from one another in their spawning experience, based on the age at which each first becomes mature. We refer to those groups that show a common age at first maturation and a common number of previous spawning experiences as 'platoons'. For cod we assume that hatching success is 100% for the third and greater numbers of times spawning. Numbers of hatched eggs (*HATCHED*) is evaluated by the double summation:

$$HATCHED = \sum_{i=1}^{n} \sum_{j=1}^{3} N_i \cdot \overline{E_i} \cdot PM_i \cdot PSP_{i,j} \cdot HP_j \quad (3)$$

$PSP_{i,j}$ = the proportion females age *i*, spawning for the *j*th time, determined by:

$$PSP_{i,j} = \begin{cases} \dfrac{PM_i \text{-} PM_{i-1}}{PM_i} & for\ j\ =\ 1 \\[2mm] \dfrac{PM_{i-1}}{PM_i} & for\ j\ =\ 2 \\[2mm] \dfrac{PM_{i-2} + PM_{i-1}}{PM_i} & for\ j\ \geq\ 3 \end{cases} \qquad (4)$$

HP_j = the proportion of eggs hatching from first, second and third+ time spawners, irrespective of age, as described above for cod:

$$HP_j = \begin{cases} 0.13 & for\ j\ =\ 1 \\ 0.62 & for\ j\ =\ 2 \\ 1.00 & for\ j\ \geq\ 3 \end{cases} \qquad (5).$$

Numbers of viable larvae (*V-LARVAE*, defined as those having a swim bladder at day 10 after hatching) are computed from:

$$V\text{-}LARVAE = \sum_{i=1}^{n} \sum_{j=1}^{3} N_i \cdot \overline{E_i} \cdot PM_i \cdot PSP_{i,j} \cdot HP_j \cdot LS_i \quad (6)$$

LS_i = the proportion of larvae surviving at day 10 which have formed a swim bladder, resulting from spawners of age *i*. This function is determined by combining the survival at length relationships and the length/weight/age curves given in Table 1.

Table 1. Parameter estimates and data used in simulations of the effects of fishing on demographic variation in spawning success of Georges Bank cod.

Parameter	Equation or Value	Reference (Comments)
Length at Age (cm)	$Lt = 148.1 \cdot (1-exp[-0.12(t+0.616)])$	Penttila and Gifford (1976)
Length (cm) / Weight (kg)	$W = 8.10443e{-}6 \cdot L^{3.0521}$	NMFS, Woods Hole Lab., File Data
Weight (kg) / Length (cm)	$L = exp((ln(WS)+11.7231)/3.0521)$	Inverse of L/W
Stock Weight at age (WS, kg), (observed, recent)	A1=0.749, 2=1.217, 3=1.866, 4=2.882, 5=4.240, 6=5.791, 7=7.976, 8=8.881, 9=10.510, 10+=15.170	Anonymous (1997) Stable over time
Natural Mortality Rate	0.2	Pope (by acclamation)
Partial Recruitment at Age, PR, (Recent)	A1=0.0003, 2=0.1318, 3=0.5316, 4+=1.00	Anonymous (1997) Increasing over time
Fecundity (E) vs. Length (cm)	$E = 1.10 \ L^{3.28}$	Buzeta and Waiwood (1982) Gulf of St. Lawrence
% Hatching Success of Eggs (by Number of Spawnings)	First Time = 13, Second Time = 62, 3+ Times = 100	Trippel (1998) Young fish in the lab
Proportion of Larvae w/swim bladder @ day 10 vs. Egg Diameter (ED, mm)	$SB_{10} = 1/(1+(ED/1.4237)^{-16.9596})$	Marteinsdottir and Steinarsson (1998) Icelandic Fish, our fit
Egg Diameter (mm) vs. Fish Length (L, cm)	$ED = 1.6(1-exp(-0.0282 \cdot [L+7.3889]))$	Trippel et al. (1997b) Norwegian Fish, our fit
Proportion Mature at Age, PM (three historic stanzas)	1986-1996: A1=0.23, 2=0.64, 3=0.91, 4=0.98, 5+=1.00 1982-1985: A1=0.13, 2=0.47, 3=0.94, 4=0.97, 5+=1.00 1978-1981: A1=0.07, 2=0.34, 3=0.78, 4=0.96, 5+=1.00	Anonymous (1997)

Biological Reference Points for Fishery Management

One "rule of thumb" approach to biological reference points is that, on average, members of an exploited stock should spawn for an arbitrary number of times - usually at least once over their life span- taking into account overall rates of fishing and natural mortality and the partial recruitment pattern of the fishery (ICES 1997). The lifetime expected number of spawnings per recruit (*LTSR*) is given by:

$$LTSR = \frac{\sum_{i=1}^{n} N_i \cdot PM_i}{R} \qquad (7)$$

where R = number of recruits = N_1.

If the effects of maternal experience on egg hatching success are taken into account, lifetime expected number of *effective* spawnings per recruit (*LTESR*) is given by:

$$LTESR = \frac{\sum_{i=1}^{n}\sum_{j=1}^{n} N_i \cdot PM_i \cdot PSP_{i,j} \cdot HP_j}{R} \qquad (8)$$

The value of fishing mortality corresponding to median (=replacement) R/SSB (F_{med}) is computed by solving the spawning index per recruit function for the F giving the replacement $(R/SSB)^{-1}$ (Sissenwine and Shepherd 1987; ICES 1997).

A number of parametric stock-recruitment relationships have been used to calculate the maximum fishing mortality rates at which the stock can persist, associated with the curvature of the *S-R* function near the origin (Smith et al. 1993; Mace 1994; Myers et al. 1995; Myers and Barrowman 1996; ICES 1997; Myers and Mertz 1998). We illustrate the use of *S-R* functions with the Beverton and Holt model (Hilborn and Walters 1992), which can be expressed as:

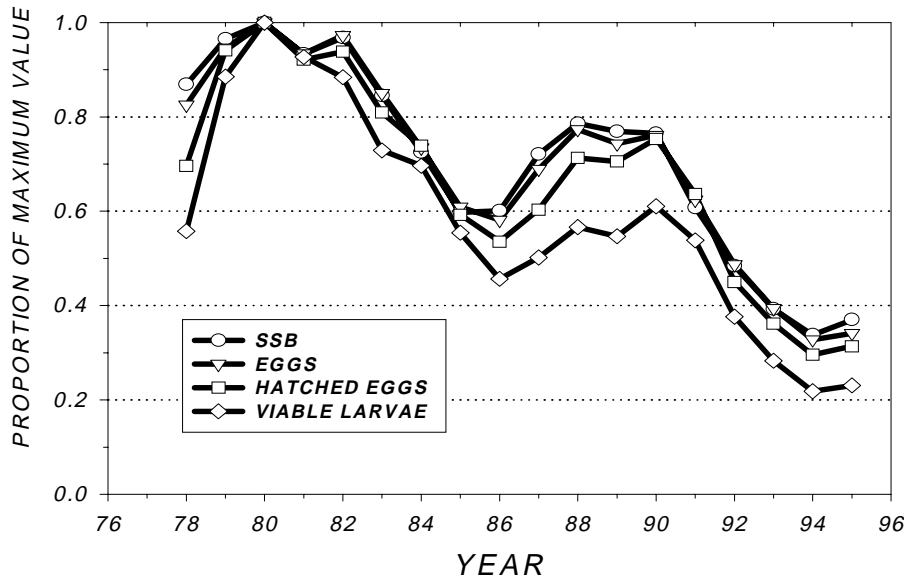$$R = \frac{\alpha \cdot SI}{\beta + SI} \qquad (9)$$

Figure 1. Calculated indices of spawning intensity for Georges Bank cod, 1978-1995. Indices are: spawning stock biomass (equation 1), total egg production (equation 2), hatched egg production (equation 3), and numbers of viable larvae (equation 6). Values are expressed as proportions of the maximum for each index (i.e. 1980 in all cases).

where R = recruits; SI = spawning index (e.g., spawning stock biomass, eggs, hatched eggs or viable larvae).

The slope of the tangent line to the predicted stock-recruitment curve at the origin is given as the quotient α/β. This tangent predicts the maximum recruits per unit spawning index (highest compensatory survival) possible for the stock. The inverse of the slope of the tangent line at the origin (β/α) is the spawning index per recruit, which can be calculated for any given fishing mortality rate as in equations 1, 2, 7 and 10 (Sissenwine and Shepherd 1987). The fishing mortality rate associated with the tangent line at the origin is the maximum at which the stock can persist, and is termed F_{crash} (ICES 1997) = $F_{extinction}$ = F_{τ} (Mace 1994).

Fitting this relationship assuming lognormal error is accomplished by:

$$\log (\ R \ ) = \ \log (\frac{\alpha \cdot SI}{\beta + SI}) \qquad (10)$$

Bias in the estimate of α is corrected by: $\hat{\alpha} = \alpha$ exp(0.5 RMSE); the slope at the origin is then $\hat{\alpha}/\beta$. We fit the lognormal form to stock-recruitment data using both SSB and viable larvae as the metrics of spawning. Results of the normal and lognormal approaches were compared.

Application to Georges Bank Cod

We re-constructed the time series of spawning metrics and calculated biological reference points for the Georges Bank cod stock (Anonymous 1997). Population dynamics parameters for the stock are given in Table 1. The time series of spawning stock biomass (equation 1) as calculated in Anonymous (1997) was contrasted with estimates of annual egg production (equation 2), hatched egg production (equation 3) and numbers of viable larvae (equation 6; Figure 2).

Trends in *HATCHED* and *V-LARVAE* differ from *SSB* and *EGGS* (in the early part of the time series and from 1986 onward) primarily due to the effects of large year classes (e.g. 1980 and 1985) which produced high proportions of first and second-time *SSB* in some years, and the increasing trend in *F*, which resulted in a progressive diminution of the proportion of older fish comprising the spawning stock. The index of viable larvae recovered to only about 60% of the maximum in the mid-late 1980s, whereas the other indices removed to about 80% of the 1980 value (Figure 1).

Under conditions of no fishing and *M*=0.2, the lifetime expected number of spawnings per age 1 recruit (*LTSR*, equation 7) is 4.24, declining to slightly less than
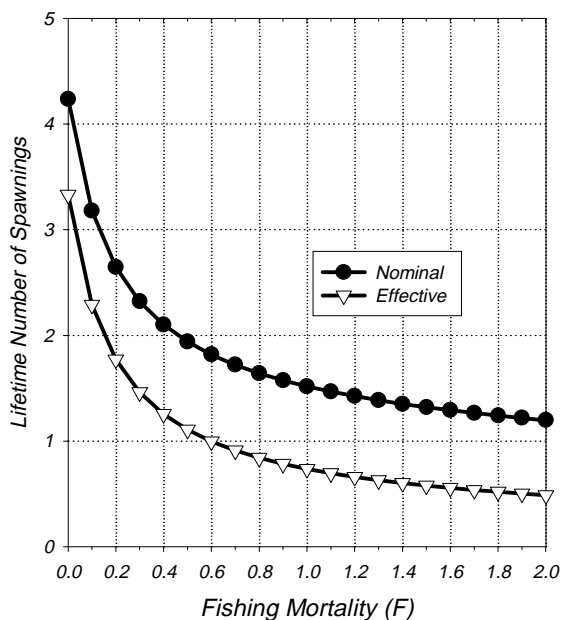
Figure 2. Expected lifetime number of spawnings per recruit for Georges Bank cod as a function of instantaneous fishing mortality rate. Nominal spawnings per recruit (equation 7) assume no differences in mortality of eggs and larvae by female size or spawning experience, while effective numbers of spawnings per recruit (equation 8) decrement the importance of first and second time spawnings.

two spawnings per recruit at F=0.5 (Figure 2). Because of the partial recruitment pattern, even at very high fishing mortality rates, the numbers of expected spawnings per recruit exceeds one. If the first and second spawnings are adjusted for maternal experience (equation 8), the expected number of effective spawnings ($LTESR$) vs. F is shifted substantially downward, declining from 3.33 at F=0, to 1.11 at F=0.5, and to 0.49 at F=2.0 (Figure 2).

The expected number of spawnings for each maturity platoon comprising the populations changes differentially with fishing mortality rate (Figure 3). This analysis is based on the partial maturity patterns observed in the most recent period (Table 1), and the total number of recruits for all maturity cohorts summing to 1. If the stock is unexploited, the maturity cohort spawning first at age 2 has the greatest expected number of lifetime spawnings (1.75), followed by those at ages 1 and 3. The maturity cohorts spawning first at ages 4 and 5 have low lifetime expected spawnings, due to their proportionally low numbers (Table 2). Increasing fishing mortality changes the expected numbers of spawnings of various maturity cohorts, resulting in about equal expectations by age 1 and age 2, and relatively low contributions by the other maturity cohorts with $F = 0.7$ or greater (Figure 2).
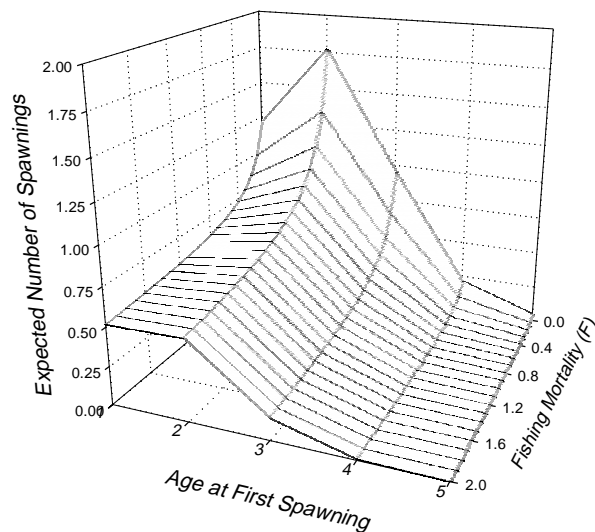

Figure 3. Expected number of spawnings per recruit for each maturity platoon for Georges Bank cod, as a function of instantaneous fishing mortality (F). Platoons are defined based upon the age at which they spawn for the first time (i.e., ages 1 to 5).
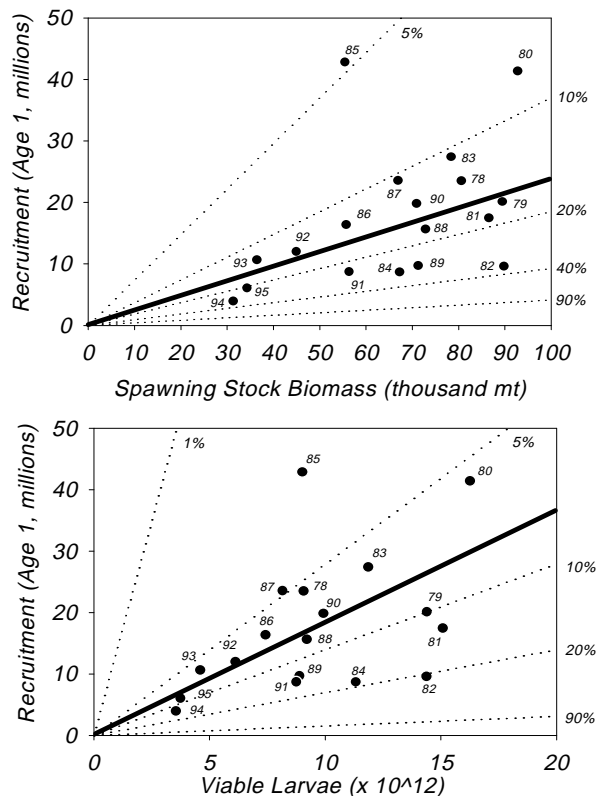

Figure 4. Stock-recruitment relationships for Georges Bank cod, 1978-1995, based on two metrics of spawning intensity. The relationship between spawning stock biomass and recruitment is plotted above. The relationship between numbers of viable larvae produced and recruitment is plotted below. In both cases, the dark line represents the median line plotted through all data. Dotted lines are associated with percentages of maximum SSB/R and Viable Larvae/R.

Table 2. Estimates of fishing mortality rate reference points for Georges Bank cod, based on calculations of F_{med} and F_{τ}. The number of successful bootstrap replicates is indicated by n=, from a maximum of 5,000.

Metric of Spawning Potential	Statistic	Fmed Reference Point			Fτ Reference Point Lognormal Error Model					Fτ Reference Point Normal Error Model				
		Fmed	%MSP	Slope	$\hat{\alpha}$	β	β/$\hat{\alpha}$	Fτ	%MSP	$\hat{\alpha}$	β	β/$\hat{\alpha}$	Fτ	%MSP
Spawning Stock Biomass	n=	5000	5000	5000	4095	4095	4095	4095	4095	2715	2715	2715	2715	2715
	Median	0.61	15.0	0.246	42288	92411	2.21	1.43	8.2	47.06	107.60	2.24	1.40	8.3
	Lower 80th CI	0.48	18.3	0.201	22211	20487	0.89	0.71	13.3	26.04	28.69	1.06	0.76	12.7
	Upper 80th CI	0.76	12.7	0.280	475643	1698488	3.62	7.71	3.3	171.69	571.24	3.42	5.40	3.9
	Point Est.	0.61	15.0	0.246	43723	95827	2.19	1.45	8.1	126.87	399.39	3.15	0.85	11.7
Viable Larvae (day 10)	n=	5000	5000	5000	4662	4662	4662	4662	4662	3969	3969	3969	3969	3969
	Median	0.57	7.7	1.831	52883	18576	0.35	0.78	4.9	42.97	12.56	0.29	0.88	4.1
	Lower 80th CI	0.47	10.1	1.397	25748	4645	0.18	0.59	7.3	24.90	4.29	0.16	0.64	6.6
	Upper 80th CI	0.65	6.4	2.208	726969	371242	0.52	1.26	2.4	159.36	71.04	0.47	1.32	2.3
	Point Est.	0.57	7.7	1.831	56458	20230	0.36	0.77	5.0	53.18	18.06	0.34	0.79	4.7

Stock-recruitment plots and estimates of F_{med} (Table 2; Figure 4) for spawning indices expressed as *SSB* and numbers of viable larvae differ from each other. Some year classes (e.g. 1978, 1989) change relative position when viable larvae is used as the spawning metric. Both *S-R* plots include isolines of percentages of the maximum spawning index per recruit (Figure 4). For *SSB* as the spawning index, the majority of data points lie between 10 and 40% of the maximum spawning potential. The point estimate of F_{med} (0.61, calculated as above) is equivalent to 15% MSP. Confidence intervals for F_{med} were determined by bootstrapping the 18 data points 5,000 times, with replacement. The bootstrap 80% confidence interval for F_{med} using *SSB* is 0.48 to 0.76 (12.7 to 18.3% MSP). Most data points for viable larvae lie between 5 to 20% MSP, with the point estimate of F_{med} (0.57 = 7.7% replacement MSP) slightly, but not significantly lower (80% confidence interval = 0.47 to 0.65), than that derived using *SSB*.

The Beverton-Holt *S-R* relationship was fit to age 1 recruitment (millions of fish) and the two indices of spawning in a non-linear least squares analysis (Table 2) using the normal and lognormal error models. The *S-R* fits were slightly better for the *R* vs. *V-LARVAE* than they were for *R*. vs. *SSB*, as measured by residual sums of squares. The point estimate of F_{τ} was higher for *R* vs. *SSB* (0.85 equivalent to 11.7% MSP) than for *R* vs. *V-LARVAE* (0.79, 4.7% MSP).

Quantiles and confidence intervals for the parameter estimates of the *S-R* curves and F_{τ} were determined by bootstrapping the 18 data points and fitting the curve to each of 5,000 potential realizations of the original data selected randomly with replacement (Hilborn and Walters 1992, p. 274). Bootstrap realizations from the lognormal model were derived by resampling the residuals from the nominal model fit, adding this error to the predicted recruitment for each observed annual spawning index value, and re-fitting the model parameters. Bootstrapping of *R* vs. *SSB* data for the normal error model produced 2,715 of 5,000 realizations (54%) wherein the model either solved or produced realistic parameter estimates (Table 2; Figure 5). The distribution of F_{τ} values is highly skewed for *SSB* (Figure 5); the median (1.4) is substantially greater than the point estimate and the 80% confidence interval is very wide (0.76 to 5.4). Bootstrapping of *R* vs. *V-LARVAE* with
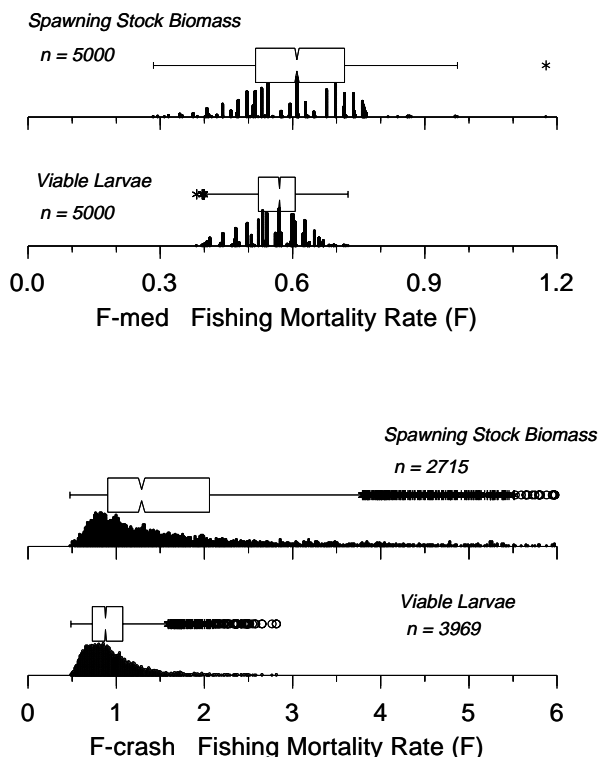
Figure 5. Frequency distribution and box plot of estimated instantaneous fishing mortality rate (F) associated with F_{med} and the slope of the stock-recruitment curve at the origin ($F_\tau = F_{crash}$), for Georges Bank cod. Results are for 5,000 bootstrap realizations of SSB and viable larvae vs. recruit data from 1978-1995, used to fit the Beverton-Holt stock recruitment relationship. Notch and ends of the box represent the median, and quartiles of the distribution, respectively.

the normal error model resulted in a higher proportion of realizations producing usable parameter estimates (3,969 cases or 79%). The distribution of values of F_τ for V-LARVAE was much less skewed (Figure 5). The median of F_τ for V-LARVAE (0.88) was close to the point estimate and the 80% confidence interval was relatively narrow (0.64 to 1.32).

The lognormal model results were similar in most regards to those derived from the normal model approach. The lognormal model could be fit to a higher proportion of SSB (0.82) and viable larvae (0.93) bootstrap realizations. Median F_τ estimates were similar to results obtained from the normal error model, and the confidence intervals were approximately equal. The only substantive difference in results between the approaches is in the point estimates using spawning stock biomass. The lognormal error model produced a substantially higher estimate (1.45) than the normal error model (0.85). These results are indicative of the highly skewed distribution of the bootstrap results and suggest

that the median of stochastic estimates is more robust than the point estimates. Results also suggest that the value of F_τ is poorly determined and likely overestimated from R vs. SSB data as compared to R vs. viable larvae.

Discussion

Our results suggest that traditional approaches for estimating biological reference points for fishery management, based on SSB as a measure of reproductive output, may systematically overestimate the potential resiliency of stocks to exploitation. If the viability of eggs or larvae is related to maternal experience, age, or size, the effective spawning potential of the stock will not be invariant for a given SSB, particularly if the age structure of the spawners has changed significantly over time. The time series of spawning metrics (SSB, total egg production, hatched eggs and viable larvae) applied for Georges Bank cod differ in those years when large year classes were spawning for their first or second time, and when F was increasing, resulting in proportionally fewer old animals in the breeding population.

The estimate of F_{med} was relatively insensitive to the choice of spawning metric (Table 2). This is not surprising since this non-parametric technique does not account for the distances that individual data points are shifted from the median line (Figure 4) due to changes in the spawning index. The time series of R/SSB and R/V-LARVAE were stationary; both spawning metrics produced adequate estimates of F_{med}, although the calculated reference point based on viable larvae was slightly lower, and was estimated more precisely (Table 2).

The estimation of maximum fishing mortality rates that the stock can withstand varies greatly with the choice of spawning metric. F_τ is, by definition, the point at which the calculated stock-recruitment relationship intersects the maximum feasible replacement survival rate (equivalent to the lowest possible %MSP and the extinction reference point). Using SSB as the spawning metric produced a median $F_\tau = 1.4$ (80% CI of 0.76 to 5.4), a value substantially greater than any fishing mortality rate the stock has experienced, notwithstanding the substantial reduction in stock size to about one third of its recent maximum (Figure 2). Using viable larvae as the spawning metric produced a median estimate of $F_\tau = 0.88$ (80% CI of 0.64 to 1.32). The latter estimate is not only preferable considering its statistical properties (Figures 9 and 10, Table 2), but is more plausible given the recent exploitation history of the stock (Figure 2). A precautionary approach to managing this stock would clearly indicate that long term replacement would not occur at $F > 0.88$, and lower if the precision of the estimate is considered.

The "rule of thumb" reference point of at least one

spawning per recruit (e.g. Myers and Mertz 1998) is seriously compromised if the first and second spawnings are discounted by the anticipated lowering of egg quality and larval viability. For the Georges Bank cod stock, the partial recruitment pattern assures at least one nominal spawning irrespective of fishing mortality rate. However, if *effective* spawnings are calculated, fishing mortality rates in excess of 0.6 result in less than one lifetime spawning per age one recruit. Our calculations also suggest that arbitrary %MSP targets (e.g. 20 to 35%; Clark 1991; Mace and Sissenwine 1993) may be inappropriate, and overly restrictive (i.e. relative to using hatched eggs or viable larvae as the spawning metric; Table 2).

The simple models proposed herein can lend new insights into the effects of exploitation on complex breeding systems that have evolved in marine fishes. Why are there up to five different maturity platoons present in the Georges Bank cod stock (and potentially more for stocks that mature later in life)? The adaptive significance of initiating breeding at different ages has not been studied intensively for cod, but is probably related to reproductive optimization, trade-offs of somatic growth at age for reproductive quality or other such considerations (Trippel et al. 1995). Clearly, variable age at first spawning is a source of diversity in a stock that has been progressively reduced by increasing exploitation (Figure 1), and intensive exploitation on juveniles and first- and second time spawners is counter to any such reproductive strategy. Indeed, the reproductive consequences of this exploitation strategy are implicated in the decline of this and similar stocks. An even more compelling question is whether or not the decline in relative reproduction by the older platoons is reversible if exploitation rates are reduced. Depending on the degree of heritability of age at first reproduction, restoring a broader representation of the various maturity platoons in the population may take generations, even if fishing mortality is reduced to very low levels.

These results suggest the directionality of biases associated with using spawning stock biomass as an estimate of reproductive output. Modeling the effects of exploitation on various metrics of spawning potential for the Georges Bank cod stock required information from studies conducted on at least four other stocks across the North Atlantic. In fact, necessary data are not available for any single Atlantic cod stock or any other fish stock to conduct these types of calculations. We expect that reproductive dynamics are at least partially local (e.g., fecundity, egg size, biochemical composition of larvae and timing of spawning). Thus, using information from one stock to apply to another is a significant source of uncertainty in our analyses. Clearly there is an urgent need to conduct additional integrated and well-designed field, laboratory and modeling stud-

ies, to evaluate the interacting effects of maternal size, age and experience on the fate of eggs and larvae. Given the universality of *SSB* as the default metric of in estimates of spawning potential, such studies should not be confined to groundfish species.

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